CHAPTER 20

THE PERMANENT FIELD RESEARCH STATION 'LES NOURAGUES' IN THE TROPICAL RAINFOREST OF FRENCH GUIANA: CURRENT PROJECTS AND PRELIMINARY RESULTS ON TREE DIVERSITY, STRUCTURE, AND DYNAMICS

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INTRODUCTION

Recently concluded and on-going studies that use plots to measure tropical forest diversity and dynamics indicate that much can be gained from plot-based approaches. In Amazonia, especially western Amazonia (Peru, Ecuador, Colombia), forest monitoring plots have been intensively worked over the past 15 years (Duivenvoorden, 1994). However, little has been published about quantitative inventories in the Guianas even though more than 60 years ago, Davis and Richards (1932–33) reported on the extremely high species richness of tropical forests based on a thorough study of a limited area in Guyana.

Knowledge of plant diversity and species richness in French Guiana stems primarily from studies conducted in the Piste de Saint-Elie area and along the coast (Sabatier and Prévost, 1990b) and in the Saül area (Oldeman, 1974; Mori and Boom, 1987). The AUBLET database (Hoff *et al.*, 1989) has noticeably improved the availability of botanical data.

Establishment of Les Nouragues field station in 1987 provided appropriate conditions for plant diversity studies. The station is part of a French-sponsored program dedicated to studying natural regeneration processes in the forest, with special reference to seed dispersal by vertebrates (Charles-Dominique, 1986, 1993, 1994; Erard *et al.*, 1989; Forget, 1990, 1992; Julien-Laferrière, 1993; Julliot and Sabatier, 1993; Théry and Larpin, 1993; Erard and Théry, 1994; Zhang, 1995; Julliot, 1996; Simmen and Sabatier, 1996). Another multi-disciplinary project (ECOFIT) is dedicated to understanding relationships among present-day diversity and recent climatic and vegetative history. Thus, the various studies underway at Nouragues use a multi-disciplinary approach that includes both contemporary evidence (species demography, spatial distribution, tree-fall gap dynamics, light measurements, seed dispersal, pedology, soil microarthropods, worms, etc.) as well as historical data (palynology, charcoal analysis, and archaeology). Improving the knowledge of floristics and structure in the area was needed to support current studies. The tree inventory program was started in 1992.

In this paper, we briefly describe the station and its current botanical projects, then present preliminary results from the projects concerning plant diversity, forest structure, and dynamics.

LES NOURAGUES

Approximately 80% of French Guiana consists of dense evergreen rain forest that is relatively intact. Les Nouragues field station is located in an undisturbed area a few kilometers (km) removed from a former temporary camp used by biologists of the Museum National d'Histoire Naturelle (Paris) along the River Arataye to study the ecology of terrestrial vertebrates (Figure 20.1) The station was named after a group of Amerindians, the Nouragues, who inhabited the area until about 200 years ago (Grillet, 1682; Grenand in Boyé *et al.*, 1979). It appears that Les Nouragues has been free of human influence since that time. This piece of a vast primary forest is included in a 1000-km² area that recently became the first fully protected forest area in French Guiana.

The geographic position of the station is 4° 5'N, 52° 42'W. General climatic conditions in French Guiana have been described by Boyé *et al.*, (1979). The salient features are annual average rainfall of about 3 m, annual average temperature of 26 °C, and a long wet season lasting from December to August that is often punctuated by a short, drier episode in late February or early March. Meteorological data have been recorded at the site since 1987. In March 1992, automatic recording (LICOR LI 1200) was instigated to ensure daily records of more reliable data for rainfall, temperature (Figure 20.2), and the quantity of sunlight.

The study area (Figure 20.3) lies at the base of a granitic dome (inselberg) and consists of two patches of land sloping upward from both sides of a creek that runs along a break separating two geologically different areas belonging to the precambrian Guianan shield. To the east, the substrate comprises metamorphic rocks – called 'Roches vertes' by the local people – in the series Paramaca; clayey soil covers the rocks. To the west, granite and crystalline rocks of the series Caraibe are partly covered with sandy clay soil.

The field station at Nouragues is rather isolated and this restricts access and hence disrtubance of the forest. A trail system about 35 km in length winds through the area; about half of it is in the grid of 100 1-ha monitoring plots. The easily accessible vegetation types vary from high, dense, *terra firme* old-growth forest to swamp forest (with *Euterpe* palm), low forest with lianas, liana forest, bamboo savanna, low forest surrounding the inselberg, and rock savanna. Observations in the canopy are possible from any of the 16 permanent platforms installed in emergent trees, three of which are connected by a 100-m long canopy walkway.

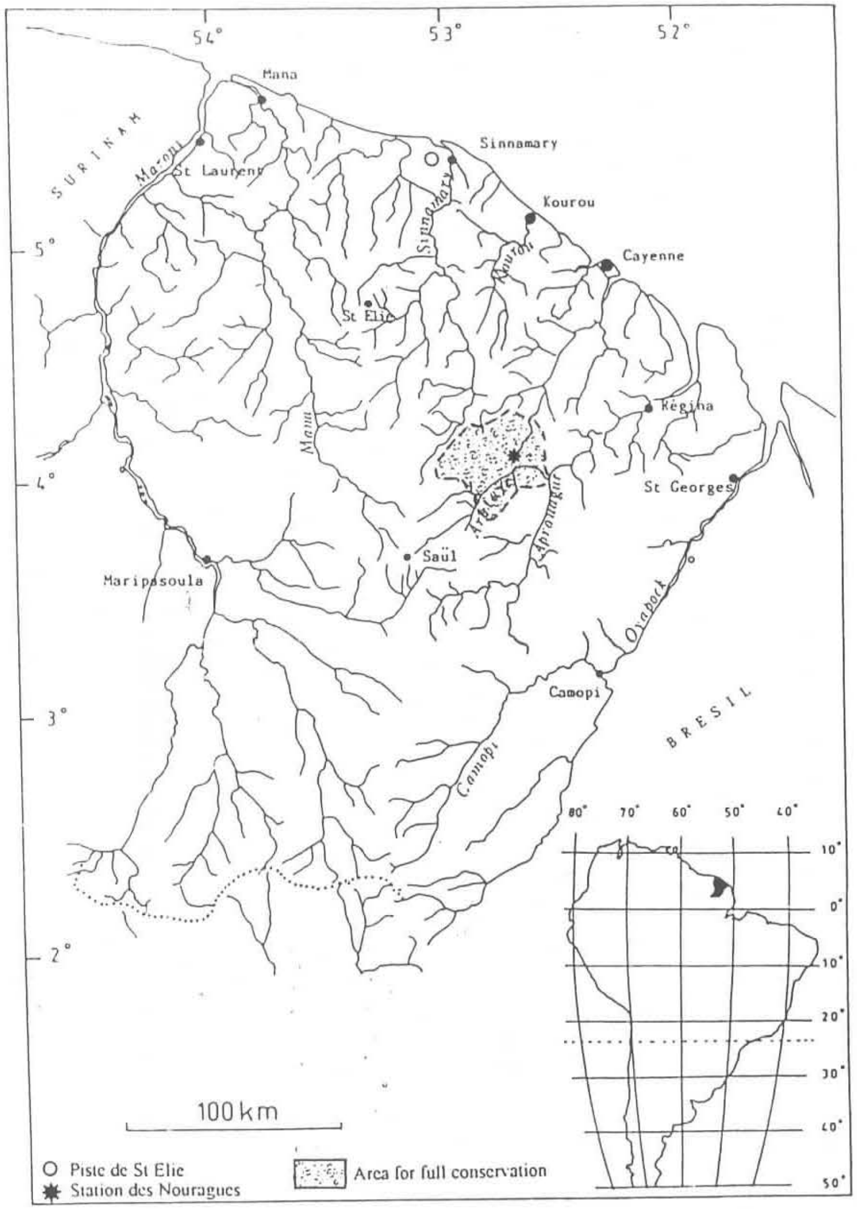

Figure 20.1 French Guiana and geographical location of Les Nouragues station

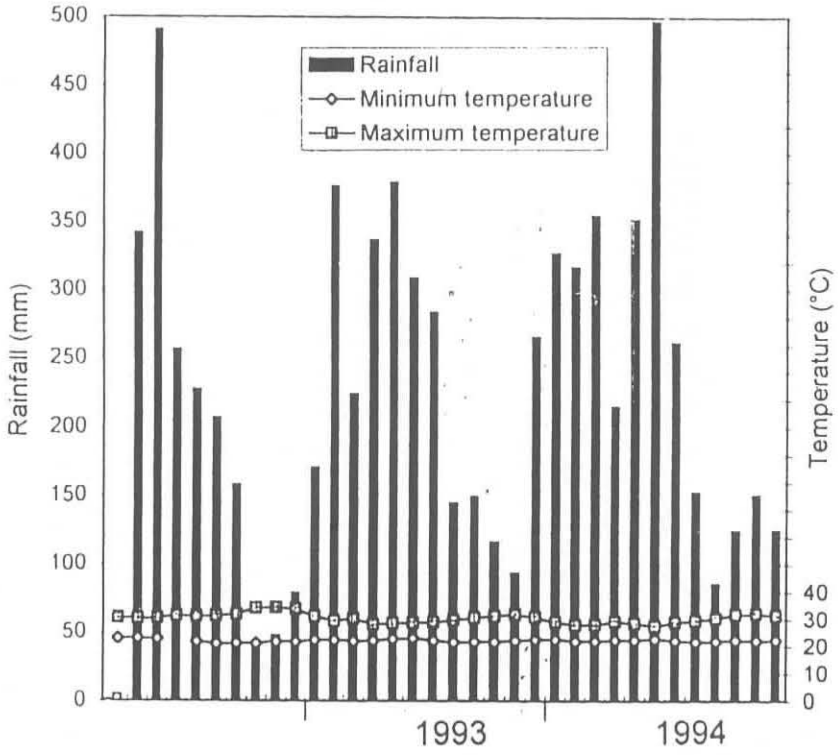

Figure 20.2 Average monthly rainfall and temperatures recorded at Les Nouragues station, 1992–1994

FLORISTIC INVENTORY OF THE NOURAGUES AREA

Plant collections in the Arataye River area before 1986 resulted from random collecting and the tree inventory of a 6-ha plot located several km away from the present station. From the Cayenne Herbarium database (AUBLET; Hoff *et al.*, 1989), a preliminary checklist of vascular plants recorded from a large area of about 50 000 ha (including Les Nouragues) was prepared. Serious improvements in knowledge of plant diversity in the Nouragues area have come about because of a botanical study of the inselberg's vegetation and the tree inventory in dense forest. Floristic data are managed at Brunoy, where the reference collection (herbarium specimens and fruit collections) is stored.

More than 1200 species of Spermatophytes have been recorded to date in the area (list available from lead author). They belong to 123 families of Angiosperms and Gnetales. The most speciose flowering plant families in the area are noted in Figure 20.4. A comparison with other long-term study sites (see map in Figure 20.1) shows that although only about 2600 specimens have been collected, Les Nouragues is likely to possess a high species diversity. The number of species

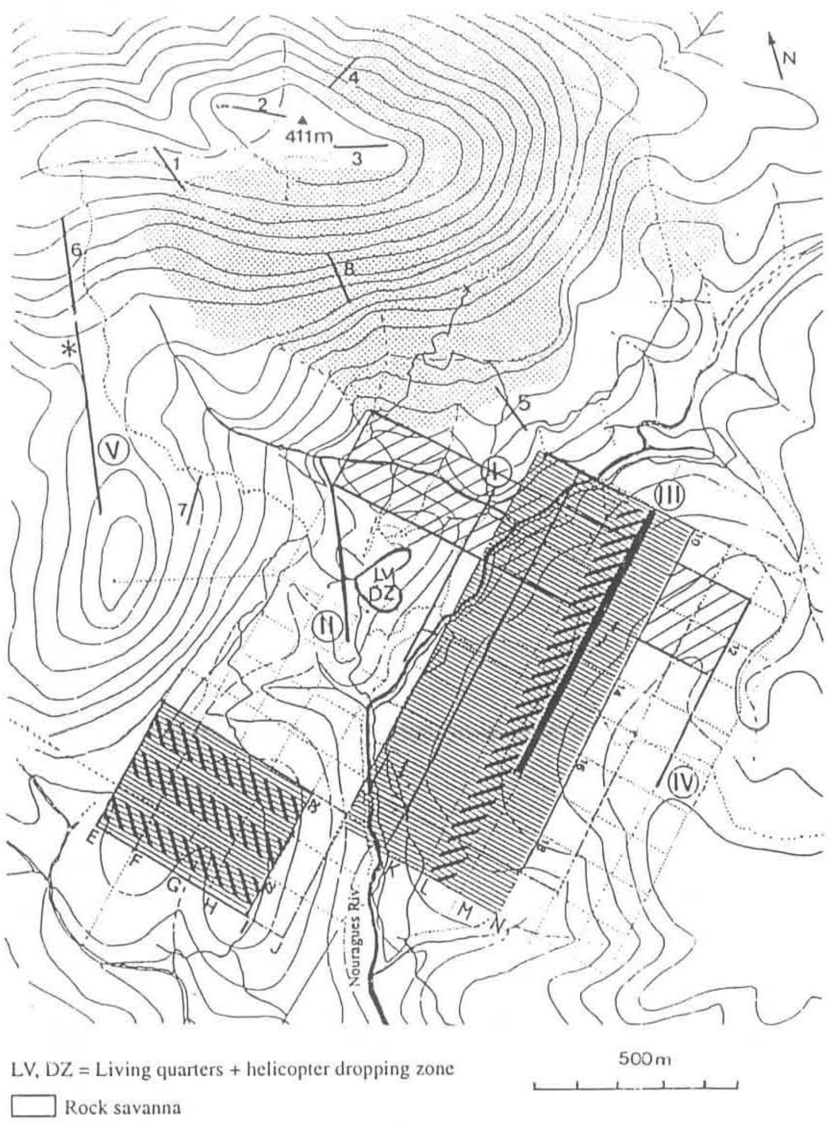

Figure 20.3 Les Nouragues, the study area. Hatched plots: inventory completed for trees ≥ 30 cm dbh; double hatched plots: inventory completed for all trees ≥ 10 cm dbh; transects 1 through 8: study of the inselberg low forests (DL); transects noted I through V: floristic inventories by Sabatier and Prévost (see text)

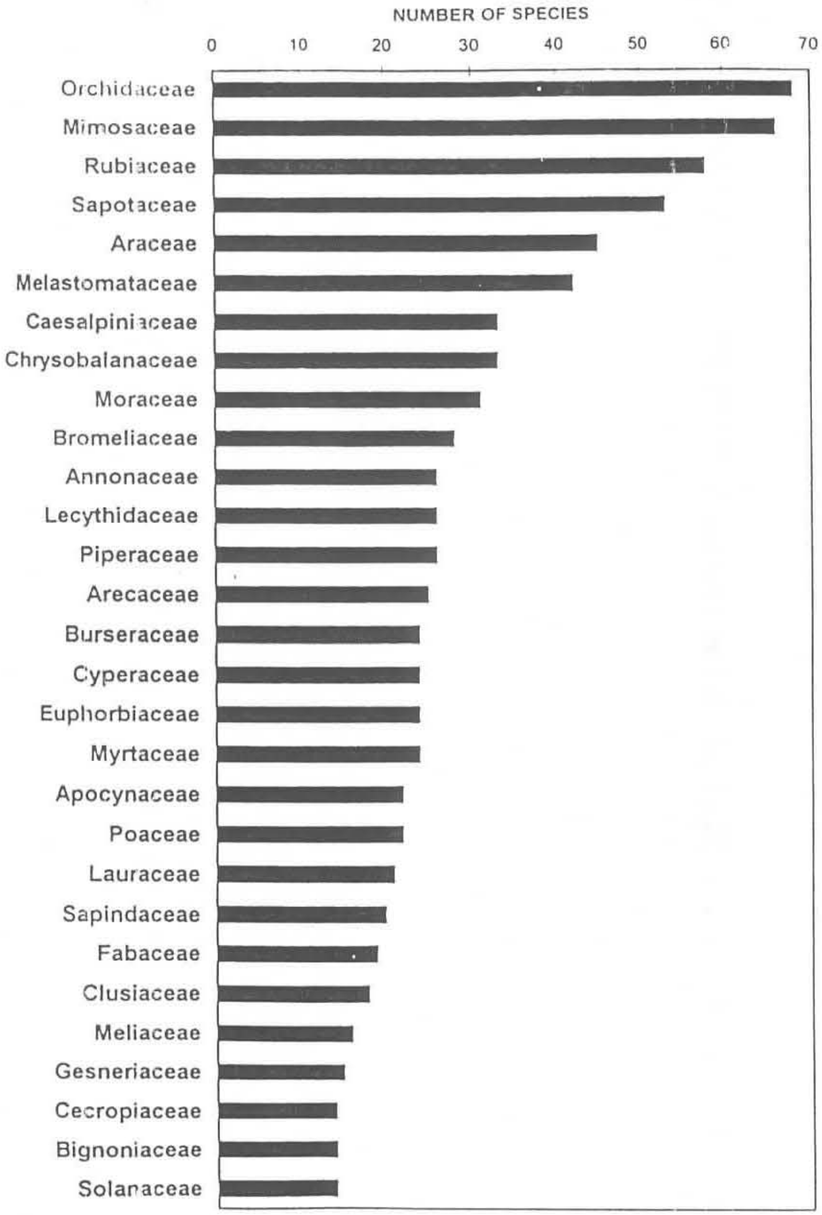

Figure 20.4 Present floristic knowledge at Les Nouragues. The most important families contain ≥ 1% of species

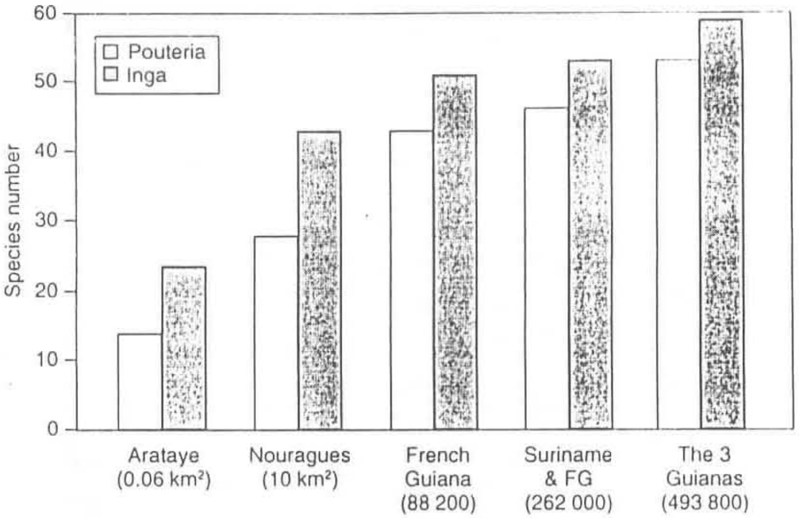

Figure 20.5 Number of species of two well-known genera at Les Nouragues compared with other areas at different scales (km²)

recorded is almost as high as at Piste-de-Saint-Elie (1420 species) where active collections have gone on for more than 20 years (about 6500 specimens collected) On the other hand, the Saül area, approximately 100 km away and considered species rich (de Granville *et al.*, 1995), has almost twice as many species (2270) as Nouragues. However, at Saül six times as many specimens (> 15 000) have been collected. Comparing the species numbers of two well-known genera, *Inga* and *Pouteria*, recorded from Les Nouragues and from larger areas (Figure 20.5) also points to high species richness at the station. Moreover, this pattern supports the theory that sound inventories in species-rich areas are an asset in floristic and taxonomic studies.

INSELBERG FOREST COMMUNITIES: STRUCTURE AND FLORISTICS

The inselberg near to the station is part of a chain of moderately elevated hills, called 'montagnes Balenfois', averaging 450 m in elevation. While other summits in the chain are covered with forest, the vegetation of the Nouragues inselberg (411 m in elevation) consists primarily of rock savanna (a mosaic with areas of naked rocks and open communities such as bromeliad mats, ephemeral rock pools, grasses, and isolated *Clusia* shrubby thickets) (Sarthou and Grimaldi, 1992) and low forests that generally form a transitional belt between the high dense rain forest and the rock savanna, but which may also occur as patches included in high forest or as clumps isolated in rock savanna areas even at the top of the dome. The analysis of physiognomy, structure, and floristic composition carried out in different sites of the inselberg low forests (Larpin, 1993; Théry and Larpin, 1993) provided detailed data contributing to the description of original features of this particular vegetation.

Methods

Because of the gradient observed from high, dense rain forest to rock savanna, transects crossing the low forests have been considered the most accurate method for use in describing plant diversity and structure of these forests. This study was carried out primarily at eight sites (Figure 20.3.), three – 1, 2, and 5 – which follow the gradient from high forest to savanna. The others cut across low forest patches enclosed either in high forest (6 and 7) or in rock savanna (3, 4 and 8). Plots of four different sizes were established along the transects, with a total area of 1.3 ha (Figure 20.6). The botanical inventory was conducted at each of the four size levels. A length of 100 m proved to be suitable for the transects, as both low forest patches and the distance between high forest and rock savanna through the low forest usually did not exceed this length.

In addition to cartography and normal size measures – diameter at breast height (dbh) and height – other data, including phenology and inclination of the trunks, were recorded. Botanical identification of the 489 herbarium specimens collected was carried out in the Herbarium at Cayenne. Data analysis was facilitated using the AUBLET database (Hoff *et al.*, 1989).

Plant diversity of the low inselberg forests

Structure

Structural data recorded in each of the five sampling transects for stems ≥ 10 cm dbh were as follows: densities ranged from 867 to 1858 stems/ha and basal areas from 30.6 to 47.3 m^2/ha; average tree heights ranged from 12.5 to 15.3 m and average dbh from 14.3 to 21.7 cm. These low forests proved to be extremely dense when compared to nearby high forests, where densities/ha for size class ≥ 10 cm dbh ranged from about 470 to 570 (Sabatier and Prévost, 1990a, present study). The density was also high compared to other forests in Guiana or Amazonia. Basal areas reached relatively high values, similar to those measured in high, dense forest (30 to 45 m^2/ha), partly because of the frequent occurrence of multi-stemmed trees (Figure 20.7) that are a particular feature of these forests resulting from adaptation to diverse constraining conditions.

Floristic and habit diversity

The botanical inventory included the entire gradient from high forest to rock savanna and low forest. Five hundred and thirty-three species were recorded, belonging to 95 families and 268 genera (available from lead author). Species

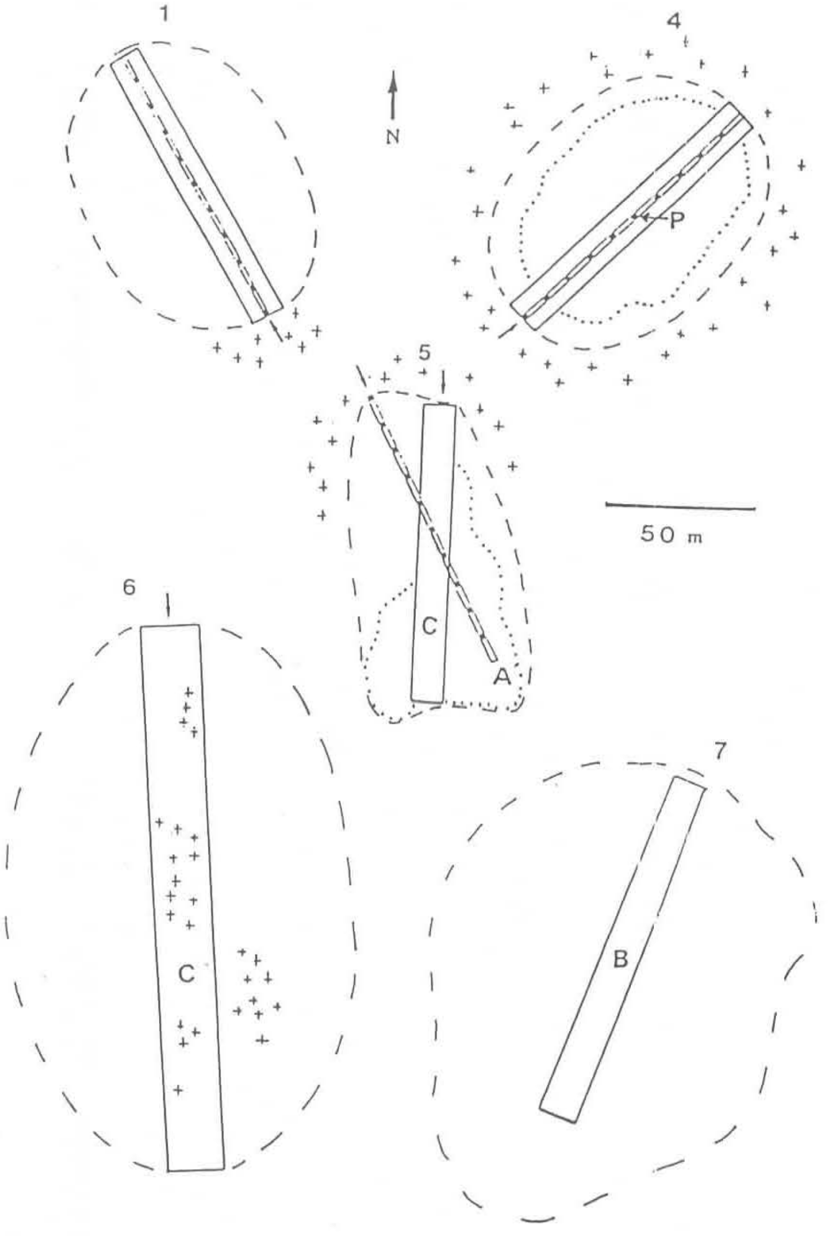

Figure 20.6 Sampling vegetation of the low forest of the inselberg in differently sized transects. A plots (100 m × 2 m): all stems ≥ 1 m in height; B plots (120 m × 10 m; 100 m × 10 m): all stems ≥ 5 cm dbh: C plots (5 100-m × 12-m transects; one 180-m × 20-m transect): all stems ≥ 10 cm dbh; P plots (5 × 11 mini-plots totalling 4 m^2): all seedlings and stems < 1 m in height. Crosses represent granitic rock outcrops

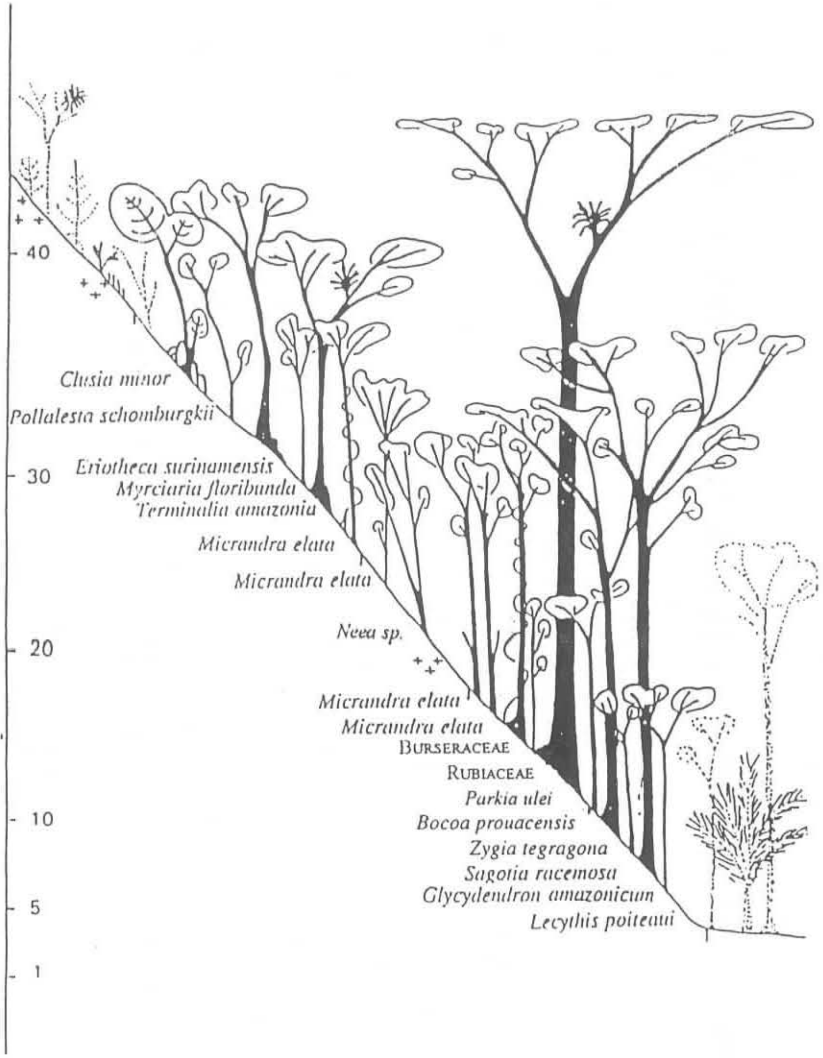

Figure 20.7 Profile diagram of the vegetation of the low forests of the inselberg

habit distribution is shown in Figure 20.8 for the 386 woody species (including 10 palms) and 147 herbaceous species (including 24 pteridophytes)

The most diverse flowering plant families are listed in Table 20.1. Only 10 genera were represented by more than four species: *Erythroxylum* with five species; *Tillandsia* with six; *Inga, Licania, Maxillaria*, and *Myrcia*, each with seven; *Eugenia, Philodendron*, and *Pouteria*, each with eight; and *Psychotria* with 10.

Table 20.1 The most speciose families of the low forest of the inselberg

Family	*Number of species*	*Number of genera*
Woody		
Myrtaceae	33	5
Sapotaceae	21	5
Mimosaceae	15	5
Apocynaceae	13	8
Arecaceae	12	7
Euphorbiaceae	11	8
Annonaceae	11	6
Caesalpiniaceae	10	5
Clusiaceae	8	5
Flacourtiaceae	6	5
Herbaceous		
Orchidaceae	50	29
Bromeliaceae	26	12
Araceae	14	6
Mixed		
Rubiaceae	36	13
Melastomataceae	14	7

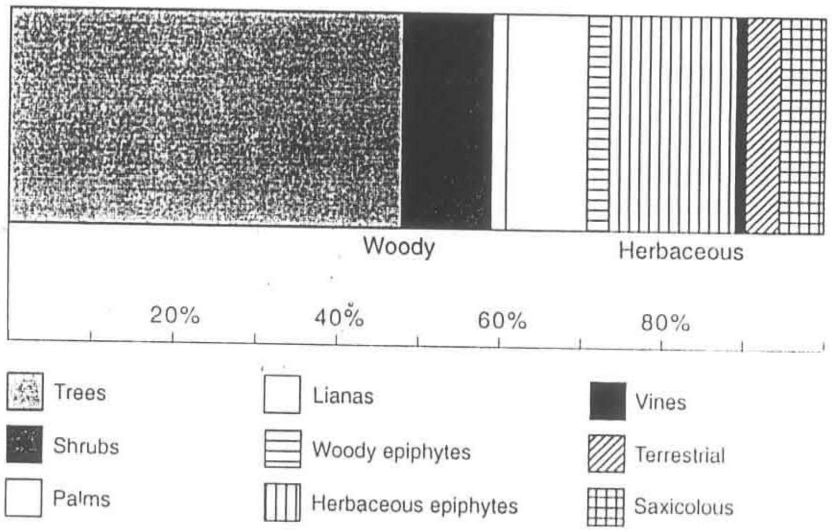

Figure 20.8 Species habit distribution in the low forests of the inselberg

Several tree species were characteristic of the flora of these forests. In the mixed transitional forest at the base of the gradient, *Calyptranthes lepida, Duroia longiflora, Cupania diphylla, Protium heptaphyllum, Licania hypoleuca, L. irwinii, Lecythis poiteaui, Sacoglottis guianensis, zygia tetragona*, and *Inga lateriflora* were found. In the contiguous low forest, common species included *Eriotheca surinamensis, Roupala montana, Terminalia amazonia* (all three anemochorous), several myrts (*Myrciaria sp., Myrcia citrifolia M. fallax, M. sylvatica*, and *Eugenia marowynensis*), three *Inga* species (*I. lateriflora, I. virgultosa*, and *I. cayennensis*), two unidentified Nyctaginaceae, and *Cassipourea guianensis*. A few species such as *Ternstroemia dentata, Pogonophora schomburgkiana, Erythroxylum squamatum, Moronobea coccinea, Humiria balsamifera, Schistostemon dichotomum*, and *Esenbeckia grandiflora* were locally clumped. Some species, including *Eriotheca surinamensis, Terminalia amazonia*, and *Micrandra brownsbergensis*, were growing on extremely thin soil and even on the granitic rock. In addition to the two unidentified members of the Nyctaginaceae, some species of the genera *Eugenia, Myrciaria, Ocotea*, and *Maytenus* remain uncertain.

Most of the common species – nearly all Myrtaceae, *Eriotheca surinamensis, Inga virgultosa, I. cayennensis, Terminalia amazonia*, etc. – in the low forests were not found in nearby high forest. A few species occured in both forests, especially *Cassipourea guianensis*, which is common throughout the high forest understory.

Characteristic shrubs included *Clusia minor* and *C. nemorosa*, the dominant species in the shrubby thickets occurring in the upper part of the gradient. *Myrcia saxatilis* was always associated with the clusias, while several other Myrtaceae were found lower in the contiguous low forest; *Eugenia ramiflora, Myrcia guianensis*, and *M. sylvatica* were the most common of these species. Among the many other shrubby species, the most common were *Ouratea leblondii, Miconia ciliata, Psychotria hoffmannseggiana, Pollalesta schomburgkii*, and *Cybianthus guianensis*.

The importance of Myrtaceae was a major aspect of the low transitional forests. The abilities of members of this family to adapt to constraining conditions in tropical climates have long been noted throughout the world as summarized by Larpin (1993), who recorded 33 myrtaceous species in the low inselberg forests. Myrtaceae dominated this particular flora in the study area, both in relation to diversity (16% to 17% relative diversity for all stems > 1 m height) and abundance (30% to 50% relative densities for the same size classes). Unfortunately, the poor taxonomic knowledge of this diverse family means only half of the species and two-thirds of the genera were named. Further discussion involving evolutionary aspects of diversification or biogeography for this family would therefore be highly speculative.

While woody lianas species were few, some may have been locally abundant. The most common were *Heteropterys sp.*, two unidentified species of *Coccoloba*, and *Securidaca uniflora*. Also often found were *Salacia impressifolia* and *Moutabea guianensis*.

Epiphytes included some woody species, among which were the ericaceous *Cavendishia callista, Satyria cerander*, and *Sphyrospermum cordifolium*. Herbaceous epiphytes included 44 of the 50 orchid species (list available from lead author). The importance of the epiphytes in these particular low forests must be emphasized. De Granville (1978) already noticed similarities between such vegetation and the lower part of the high forest canopy, a zone described as 'lower-canopy' by ter Steege and Cornelissen (1989). The forest sites with the highest densities of epiphytes were not those growing on the richest and thickest soils, as suggested by Gentry and Dodson (1988). To the contrary, epiphytes were proliferating primarily in areas with very thin or no soil where low forest covered outcropping granitic rock.

Floristic affinities

The inselberg forests clearly exhibited a particular flora when compared to nearby high, dense forest. Only about 25% of the tree species of the inselberg forests were also found in high, dense forest. Among inselberg species not occurring in high forest, several were found in other similar places (additional inselbergs and granitic outcrops) or in open areas such as coastal savannas or savannas of southern Guyana and Suriname. Most (*Cochlospermum orinocense, Inga virgultosa, Tabebuia capitata, Roupala montana, Esenbeckia cowanii, Ternstroemia dentata, Ernestia granvillei*, and *Sauvagesia aliciae*) were geographically restricted to the Guianas and adjacent areas. Similar distribution patterns were exhibited by herbaceous species, including *Pitcairnia geyskesii, Cyrtopodium andersonii, Ananas nanus*, and *Stelestylis surinamensis*, recorded from the rock savanna. A few species such as *Inga lateriflora* and *Licania irwinii* found in the low forest of the Nouragues inselberg were previously known only from the white sand forests of the Guianas. Very few species (*Inga cayennensis* and *Licania hypoleuca*) had wider geographic extension, reaching southern or western Amazonia. Even fewer were species also known from rocky riparian habitats (river rapids), including *Calliandra surinamensis*, or from very wet montane or cloud forests (*Licania hypoleuca, Cybianthus guianensis* ssp. *pseudoicacoreus*, and *Miconia holosericea*)

Finally, this thorough inventory of Nouragues' low forest vegetation provided the opportunity to collect a set of extremely rare or new species, among which were orchids, three mimosoids (two new species of the genus *Zygia*), *Eriotheca surinamensis, Micrandra brownsbergensis, Esenbeckia grandiflora*, and *Syagrus stratincola*.

THE NOURAGUES TREE INVENTORY PROGRAM

Methods

The tree inventory program began in 1992 in the 100 1-ha plots distributed on both sides of the creek (Figure 20.3). Field work included mapping and numbering the trees, measuring dbh, recording the local name, and gathering data for botanical identification. According to the initial project, all trees ≥ 30 cm dbh were to be inventoried. In addition, all stems ≥ 10 cm dbh were recorded in two portions of the larger area. First, 12 contiguous 1-ha plots in the western area were studied as part of research on forest dynamics, including tree-fall gap dynamics analysis, in concert with colleagues at the Wageningen Agricultural University (e.g. Sterck *et al.*, 1992; Van der Meer *et al.*, 1994; Riera, 1995; Van der Meer and Bongers, 1996). Second, a 10-ha plot on the opposite side of the creek was included as part of research on forest structure, using radar transported by helicopter (Riéra *et al.*, 1994). Nearly four ha of this plot have been extensively analyzed (Sabatier and Prévost, 1994 unpublished data) to provide additional structural and floristic data.

Special attention was paid to particular taxa because they were expected to be interesting given a previously established framework. Inventory and mapping of these taxa, including the genera *Cecropia, Pourouma, Inga, Carapa, Vouacapoua*, and *Eperua*, were conducted for all stems ≥ 10 cm dbh in the 100-ha area.

The use of 100-m long strings, tagged with colored tape every 10 m, facilitated cartography work. The strings delineated temporary 100 × 10-m strips and 100-m^2 mini-plots that could be studied in succession. Each tree was given a unique number to indicate in which plot it occurred. Two Surinamese maroons of the Saramaca ethnic group provided local names for the species. Specimen collection voucher was done when possible; staff climbed trees to gather the specimens. All data, including scoring of geographic coordinates, were entered into computers. Maps were edited and printed through TREEDRAW, a software program written by R.P. Leersnijder at Wageningen Agricultural University (The Netherlands).

State of inventory progress and preliminary results

For trees ≥ 30 cm dbh, the first step (tagging, recording dbh, and mapping) was scheduled for completion in late 1996 (Figure 20.3). The survey for botanical identification was finished on a 9-ha plot (100 × 900 m) for adult canopy species ≥ 30 cm dbh, in 1995.

Structural data and distribution of forest types in the 100-ha area

The occurrence of physiognomically different forest zones in the Nouragues was noted above. Mapping the surfaces occupied by these zones throughout the 100-ha area was the result of observations of physiognomical criteria made by several researchers, including an ornithologist who prepared Figure 20.9 to provide a structural basis for studying the use of space by understory bird communities. Forest zones were distinguished using the following qualitative criteria: canopy height, density of the understory, and density of lianas. The first zone was high mature forest, with a fairly open understory and two subsets according to canopy height (zone 1 with average canopy height of 35 m and zone 2 with an average of 25 m in height). The next zone was low forest, with many lianas and two subsets (zone 3 with average canopy height of 12 m, a few stems reaching 30 cm dbh (see below), and many trees overloaded with lianas and dense understory; zone 4, dominated by lianas with imbricated liana stems at ground level, making the understory extremely difficult to access). Zone 5

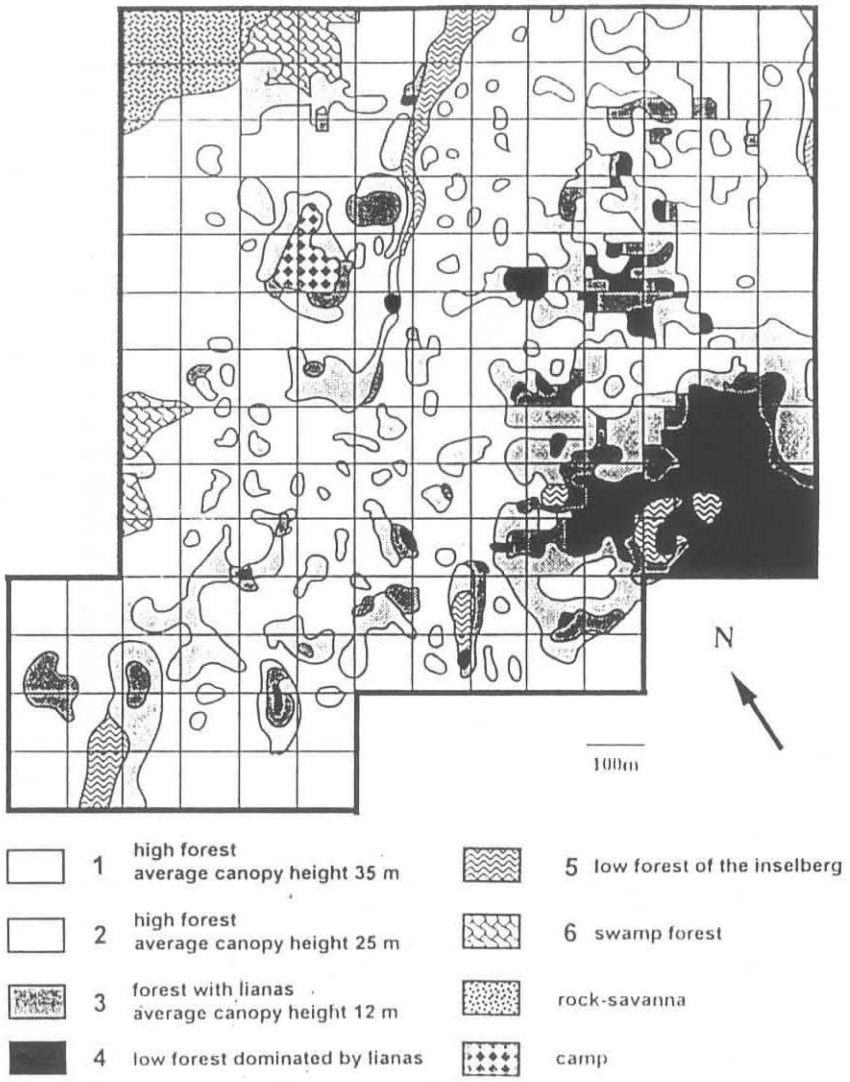
N
100m
1 high forest average canopy height 35 m
2 high forest average canopy height 25 m
3 forest with lianas average canopy height 12 m
4 low forest dominated by lianas
5 low forest of the inselberg
6 swamp forest
rock-savanna
camp

Figure 20.9 Forest types in the study area. See text

corresponded to the low forests of the inselberg, described above. Zone 6 consisted of swamp forest dominated by *Euterpe* palms. In the future, with an increase in structural quantitative and floristic data, especially for smaller stems (< 30 cm dbh) and lianas, the tree inventories should provide formalized descriptions of the forest types.

Variation in density and basal areas for size classes ≥ 40 cm dbh and ≥ 30 cm dbh reflected strong structural heterogeneity in the eastern part of the 40-ha sample area, which was obviously related to the presence of patches of disturbed forest (low forest dominated with lianas or liana forest). Similarly, low values of basal area were related to the low number of large trees. The western sample (12 ha) appeared much more homogeneous; structural data were similar to those of the northern part of the 40-ha plot. The distribution pattern (Figure 20.10) suggested that the deficient size classes in the liana forest were those ≥ 50 cm dbh.

For trees ≥ 10 cm dbh, density ranged from 488 to 570 stems/ha on the eastern 40-ha plot. Densities were very similar on the 12-plot sample where there was no disturbed forest. Hence, there appeared to be no strong influence of the occurrence of the liana forest on densities when all size classes were considered. Similar densities (473 to 563 stems/ha) were found by Sabatier and Prévost (1990a) for four of the five plots they studied, with the fifth plot showing density up to 882 stems/ha (transect v in Figure 20.3). These numbers are somewhat lower than those recorded in central and western Amazonia – about 600 stems/ha (Gentry, 1988) between 600 and 700 stems/ha (Rankin-de-Merona *et al.*, 1990), 637 stems/ha (Rankin-de-Merona *et al.*, 1992), and 734 stems/ha (Balslev and Renner, 1989). Calculated basal areas/ha ranged from 30 to 43 m²/ha, slightly lower than the 53 m²/ha found by Mori and Boom (1987) in the vicinity of Saül, but higher than the 27 to 34 m²/ha noted by Rankin-de-Merona *et al.*, (1990) in forest plots in Central Amazonia.

Floristic composition and tree diversity

A list of species recorded from the general tree inventory are available from lead author. The most abundant canopy trees recorded on the 100-ha area included members of the families Leguminosae (especially *Eperua falcata* and *Vouacapoua americana*), Sapotaceae, Burseraceae, Chrysobalanaceae, Lecythidaceae, Rubiaceae, Vochysiaceae, and Nyctaginaceae.

Botanical analyses of trees concentrated on a 9-ha plot where 899 trees ≥ 30 cm dbh were found belonging to 33 families of Dicotyledons (Figure 20.11). One hundred and sixty-eight species of mature canopy trees were recorded in this area, 70% of which were given one of the 145 species names identified so far. The species number/ha ranged from 39 to 87. The family importance value (FIV; Mori *et al.*, 1983) was calculated for all families recorded on the plot (Figure 20.11); 50% of the trees belonged to only four families, with the Leguminosae totaling more than 25%.

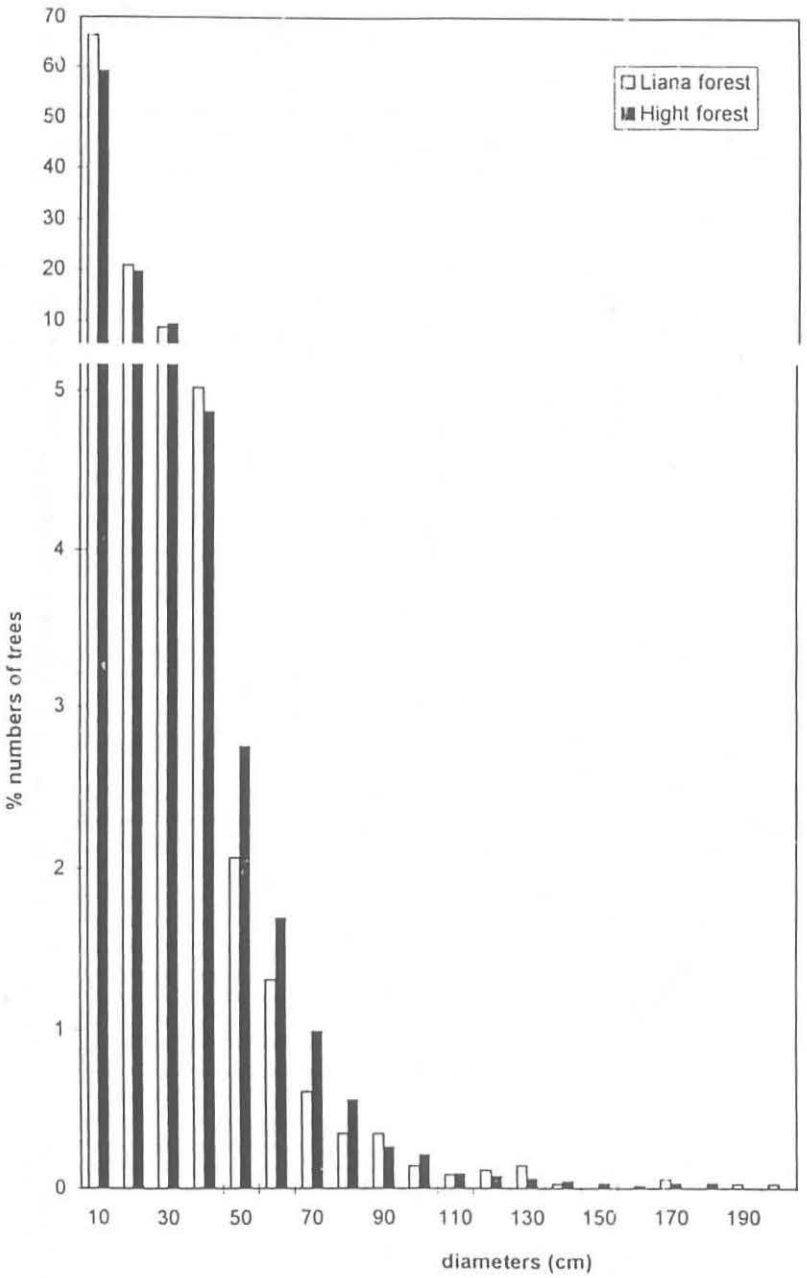

Figure 20.10 Size class distributions of diameters in two forest types. Liana forest refers to 4 1-ha plots, each covered with > 50% low forest dominated by lianas; high forest refers to 12 1-ha plots without liana forest

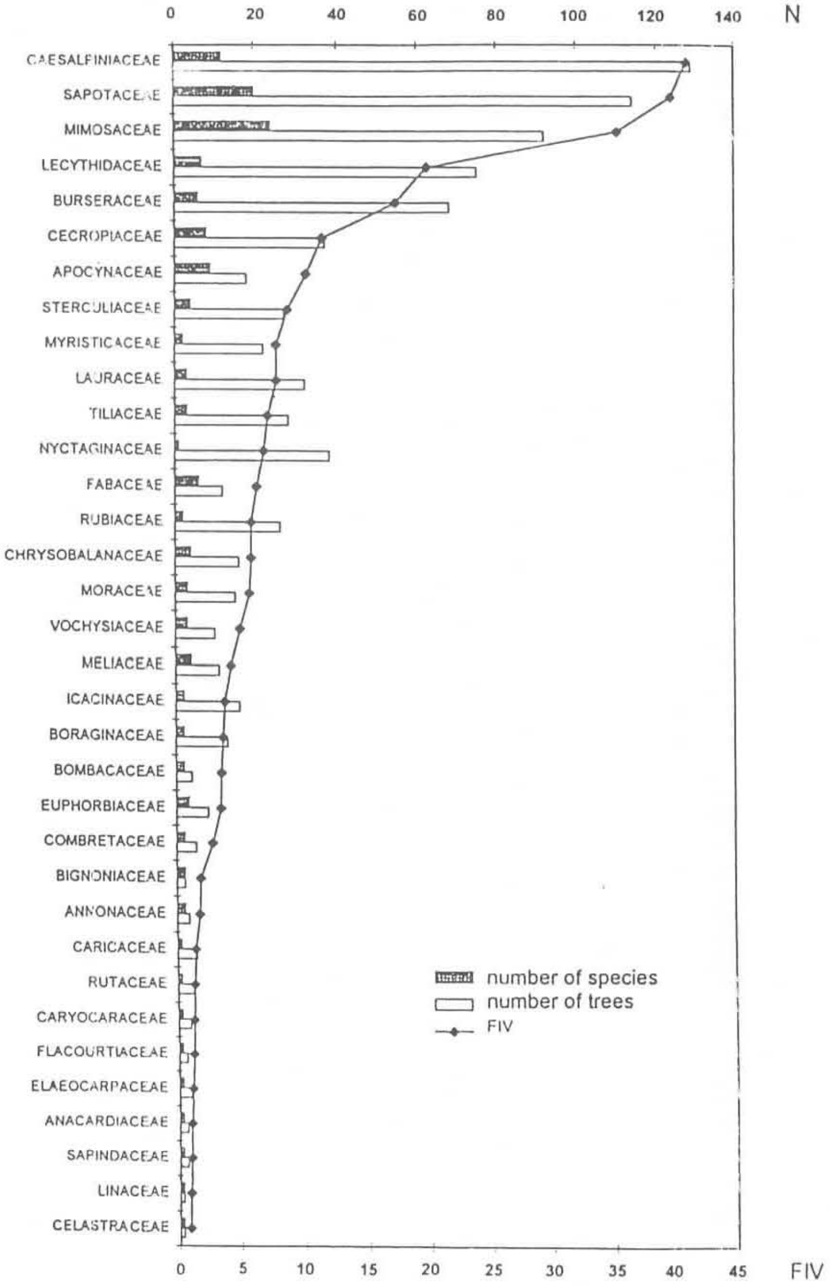

Figure 20.11 Importance of families in nine 1-ha contiguous plots (≥ 30 cm dbh; number of trees, number of individuals, Family Importance Value)

In relation to dominant families, some differences in the study area were consistent with findings of Sabatier and Prévost (1990a) in their preliminary study of five sample plots chosen in seemingly homogeneous forest areas. Lecythidaceae and Sapotaceae were always present among the five major families, while Chrysobalanaceae and Caesalpiniaceae were found on four transects, Burseraceae on two, and Mimosaceae on one. In transect V (Figure 20.3), Clusiaceae and Lauraceae were among the group of five leading families. Most tree species occur only in one or two samples, accounting for the existence of floristic mosaics.

This pattern is different from that observed in forest located only seven km away from Nouragues at the border of Arataye River, where an exhaustive inventory of a 6-ha plot was carried out from 1981 through 1984. In that sample, the five leading families were the same as at Nouragues, but Burseraceae dominated (15% of the trees). *Tetragastris altissima* was abundant, as in the forest of the vicinity of Saül (Mori and Boom, 1987). Caesalpiniaceae and Mimosaceae totaled less than 10% of vegetation, and *Vouacapoua* was absent.

Several inventories in the central Amazon region near Manaus, summarized by Rankin-de-Merona *et al.*, (1992), yielded a similar pattern of floristic composition to that of Nouragues, while Moraceae, Lauraceae and Annonaceae were among the most important families in the Manu forest in Peru (Foster, 1990).

Spatial distribution of some species and the gradient factor

The sample plot was chosen for floristic analysis because it crosses a gradual transition from high forest with clear understory to liana forest; its orientation is approximately parallel to the creek; and its topography is rather constant – no steep inclines – so that one can expect variations in species distribution to be unrelated to slope and river. In addition, preliminary pedological investigations (P. Grimaldi in P. Dupré, 1994 unpublished data) suggested a close relationship between soil and vegetation; i.e. under the high forest a typically ferralitic, thick, free-drained soil (oxisol) was found, while under the liana forest, the characteristic soil with micro-aggregated structure was also present but was much thinner, thus suggesting that this part of the forest has undergone considerable erosion.

Mapping individuals of particular species or genera in the sample area reflected the floristic heterogeneity related to the structurally distinct patches of forest (Figure 20.12). The maps also provided the basis for studies of tree/animal relationships, especially in relation to feeding and dispersal. Patterns such as the distributions of Sapotaceae and Lecythidaceae suggested that tree diversity decreased in the low forest dominated with lianas. This was not obvious when comparing species richness (for adult canopy trees ≥ 30 cm dbh), which was rather homogeneous on 8 of the 10 1-ha plots (59 to 69 species/ha) even where the extreme values included either high forest (87 species/ha) or mostly

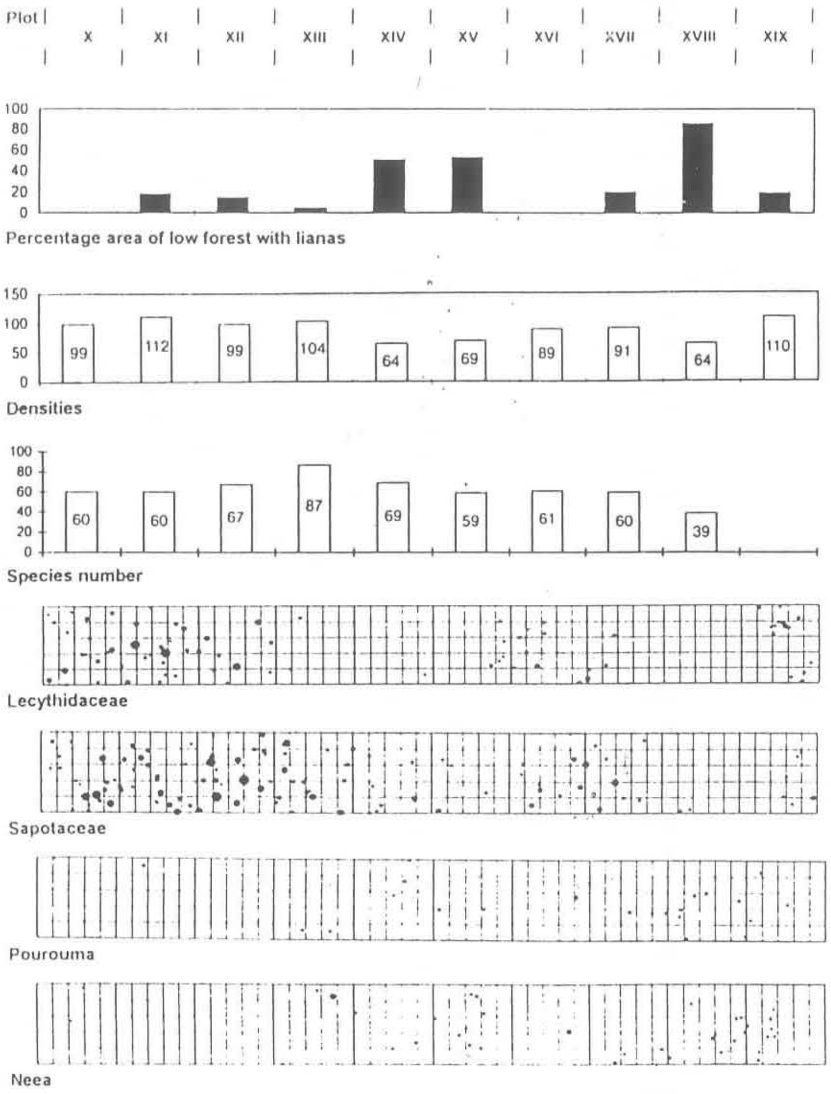

Figure 20.12 Spatial distribution of certain taxa in a 10-ha plot with reference to forest type, densities, and number of species/ha

liana forest (39 species/ha). Increased densities of trees belonging to the genera *Neea* and *Inga* and, to a lesser extent, *Pourouma*, as well as *Apeiba* and *Sterculia* in the low and liana forests, should be noted. Moreover, no species were recorded exclusively from low forest or liana forest.

Neea sp. (*N.* aff. *floribunda*, Nyctaginaceae, a species with unclear taxonomic status awaiting family treatment) required special attention. This species was particularly abundant in the low forest dominated by lianas (Figure 20.12), where it exhibited a unique feature – low, weeping branches – noted earlier by Sabatier and Prévost (1990b). According to those authors, the density of this species in the liana forest can reach up to eight stems (5 to 15 cm dbh)/ 100 m. Such data suggest strong potential of regeneration under the liana cover.

Only a few species, including *Jacaratia spinosa* and *Bagassa guianensis*, found in the low forest with lianas were also abundant in the liana forests of the Xingu River Basin analyzed by Balée and Campbell, (1990). *Astrocaryum sciophilum*, a common palm in the high forest, did not occur in the liana forest. However, *Socratea exhorrhiza* became abundant, although not as conspicuously as *Orbignyia phalerata* (Balée and Campbell, 1990). Overall species diversity seemed less rich than in the Xingu samples; in the genus *Neea*, six species were recorded at Xingu, but only one at Nouragues.

DISCUSSION

Diversity and mosaics

Various forest types occurring in the Nouragues area were described. The high mature forest was not homogeneous, and its pattern of mosaics most likely is common in Amazonian rain forests as concluded by Campbell *et al.*, (1988). The forests of central French Guiana described to date fit in two main types – Burseraceae and Caesalpiniaceae (Sabatier and Prévost, 1990b) – according to the dominant family. Both occurred in the Nouragues area along with great diversity of Sapotaceae. The reasons for the occurrence of great species diversity are still topics of debate in the neotropics (Gentry, 1990) and elsewhere (O'Brien, 1994).

Most studies carried out in French Guiana emphasize relationships between soil structure and the distribution of either particular species or forest types (Lescure and Boulet, 1985). Drainage conditions have been given special importance, with an attempt to distinguish species tolerating badly drained soils from strictly intolerant species. Species such as *Eperua falcata*, *E. grandiflora*, and *Vouacapoua americana* were involved in these analyses. These species and species of the genus *Inga* are currently being studied as part of a small-scale spatial distribution analysis of some taxa occurring in the study area (A. Joly and P. Poncy unpublished data).

Sabatier and Prévost (1990a,b) also discuss the observed variation in floristic composition of the forest plots they studied, in relation to soil criteria. Interactions with animal communities are thought by these authors to be a determining influence locally in variations, but not on a regional scale. Most studies carried out in the field of seed dispersal ecology (see p. 385) emphasize the importance of mechanisms acting within small areas, especially since seed dispersal by animals usually occurs within short distances. These mechanisms, important in 10-ha areas or smaller, are often responsible for favoring clumped distributions of the tree species.

Data available on spatial distribution of *Vouacapoua americana, Eperua falcata*, and *E. grandiflora* (see above) provide stimulating examples of what can be expected from such approaches to the estimation of the role of recent forest history in establishing mosaic patches. For example, in the study area the distribution patterns of *Eperua falcata* and *E. grandiflora*, which had especially low recolonization rates because of barochory, strongly suggested the absence of any recent disturbance. Several herbaceous or liana understory species such as members of Cyclanthaceae might provide the same kind of information (P. Blanc personal communication).

Diversity, structure, and dynamics: the liana forest

Liana forest is the third fasciation distinguished by Sabatier and Prévost (1990b) among forests growing on ferralitic soils. Its origin and dynamics are not clearly understood, but on the basis of a floristic analysis of two liana forest plots in the Xingu River Basin, Balée and Campbell (1990) hypothesized that liana forests are likely to be of anthropogenic origin because of the occurrence of many long-lived biological nomads. Sabatier and Prévost (1990b) favor an edaphic origin, arguing that these forests are mainly located on the slopes of lateritic plateaus and that steep slopes could prevent high forest from stabilizing. However, liana forest at Les Nouragues covered poorly inclined slopes, while high forest covered nearby steep slopes. According to preliminary pedological data (P. Dupré, 1994 unpublished data), close relationships can be expected between liana forest and soil, but more detailed analyses are needed in the transitional areas along the gradient. The occurrence of a thinner, ferralitic layer may result from very ancient geomorphological changes in northern Guiana (M. Grimaldi, personal communication). More recent, local causes such as forest destruction through previous human activity or climate changes must also be examined.

Evidence of previous human occupation has been found at several sites in the Nouragues area. It consists of broken earthenware pieces, polishers, and, above all, charcoal. Charcoal pieces are being studied and dated; preliminary results (Tardy, 1994) indicate long-ago human activity (dating back about 1400 years) and paleo fires (fires that occurred in previous times under drier climates; Absy *et al.*, 1991; Soubies, 1980). Consistent with former human occupation were some individuals of *Ceiba pentandra* and *Spondias mombin*, recorded from the tree inventory plots in the low forest with lianas, and a 1.5-ha bamboo patch located about 500 m from the most dense liana forest area. Such isolated bamboo patches, called 'cambrouzes', are often reported in French Guiana and

are thought to occur on the sites of previous Amerindian villages (Sastre, 1980).

Research for this study indicated that soil structure was not the primary reason for occurrence and maintenance of liana forest. Serious local and long-lasting disturbances probably led to both forest destruction and soil alteration. For example, the occurrence of a dry period at a critical stage of recruitment after strong forest disturbance might have allowed heliophilous lianas to become dominant. This would have resulted in disturbance of regeneration processes, possibly even stopping them before complete successional stages to high, mature forests were completed. *Inga* species are generally considered to belong to the early stages of forest succession. In the case of the liana forest, the abundance of *Inga* trees is not likely to indicate a young forest, as suggested by Balée and Campbell (1990). Rather, it will likely prove succession was halted, providing conditions suited for success of most *Inga* species.

In relation to dynamics and the future of the liana forest, structural data provided by the tree inventory showed that the tree population was not decreasing nor succumbing to unfavorable competition from the dominating lianas. This study found no evidence of qualitative differences in floristic composition, contrary to the low forests of the inselberg.

In any event, high forest trees fared poorly in low forests with lianas, while other taxa became abundant (several *Inga* species and *Neea* aff. *floribunda*). It is difficult to say whether these species took advantage of their ability to grow on poor or badly drained soil or to survive under a dense liana cover. *Neea* showed great ability to produce basal branching. According to Sabatier and Prévost (1990b), this species would contribute to the elevation of the liana strata and therefore to the evolution of the liana forest toward high forest. The success of many *Inga* species may also be caused by morphological plasticity, including an ability to throw out and thus prevent the trees from dying when falling or bending, similar to lianas (Putz, 1984).

We agree with Sabatier and Prévost (1990b) that the liana forest is presently a relatively stable fasciation. Whether it will return to high forest remains highly questionable. The occurrence in the liana forest of old emergent trees draped with liana tangles suggests progress of lianas against high forest. But some of the preliminary observations in this study account for recent progress of high forest against liana forest; i.e. the distribution pattern for *Inga* (data to be published elsewhere), with high densities of trees in a high forest patch surrounded by low forest with lianas; pedological observations (P. Dupré, 1994 unpublished data) that suggest the soil structure under the liana forest may intergrade in certain places with that in the adjacent high forest; and the presence of apparently old *Neea* individuals in high forest adjacent to the liana forest.

CONCLUSION

Although preliminary, the data collected during the initial years of this study showed that the Nouragues area had significant plant diversity at both alpha and beta levels, with each of the plant communities containing its own unique pattern of structure and dynamics. Our continuing studies will hopefully increase understanding of these patterns. In addition to the factors discussed, animals played an important role as seed dispersers, especially since the scale of their activities corresponded to that of the forest patches under study. Moreover, long-ago human activity as well as recent climate changes were attested in different ways and must be taken into account in the interpretation of vegetation history.

Until now, there are relatively few published data available from quantitative inventories in French Guiana. For the reasons mentioned above, and according to Condit (1995), arguments for further studies of large, long-term forest plots must still be made. Our results from Les Nouragues provide strong evidence for those arguments. The area provides ideal conditions for producing quantitative data as part of multi-disciplinary studies on natural processes at work in an undisturbed forest.

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